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CONTENTS

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ON TWO ADVANCES OF TSETSE-FLY IN CENTRAL TANGANYIKA.

By C. H. N. Jackson, D.Sc., Ph.D.

(East African Tsetse Research Organization, Shinyanga.)

1. Introduction.

More than 15 years have passed since (1933) I described one of two belts of tsetse-fly (*Glossina morsitans* Westwood) which were converging upon Singida in the Central Province of Tanganyika. Since then both belts have made further progress; the latest published account is by Swynnerton (1936), who describes both the eastern and the western advances up to the end of 1933, and indicates (Map 6) the vegetation of the country about Singida, but omits most of that portion of Kondoa District invaded by the flies. (He notes that "the thicket on the southern side, east of the Singida railway is not shown on the map." The scale of Swynnerton's map, 1 : 1,000,000, is also the scale of that accompanying the present paper.)

The area now to be considered lies between 34 and 36° E. longitude and between 4° 30′ and 5° 30′ S. latitude; the altitude varies between about 4000 and 6000 ft. The eastern half is traversed by two major step-faults with escarpments facing east: the Kondoa scarp faces across the Masai Steppe and the Singida scarp overlooks the East African Rift Valley, in which Mt. Hanang rises to 11,000 ft. The eastern portion is drained by the Bubu and Mponde rivers, which independently enter an inland drainage basin to the south. The topography is less exaggerated in the western half, where the sluggish Mwaru and Iwumbu rivers crawl westward to lose themselves in the seasonally inundated Wembere Steppe, which farther north is overlooked by the precipitous west wall of the Iramba Plateau.

The Irangi and Turu cultivation steppes, surrounding the towns of Kondoa and Singida, form bare, eroded enclaves resisting encroachment by the flies; the Singida cultivation steppe merges in the north-east into grassy plains which, like the Wembere in the west, are too open to shelter tsetse.

In the south-west of the area lies a great block of deciduous "Itigi" thicket, and outliers extend into Kondoa, especially in the south. This thicket is too dense to form a habitat for *G. morsitans*, which can barely penetrate a mile into it when leafless in the dry season (B. D. Burtt, quoted by Swynnerton, 1936). The remainder of the country consists of deciduous, short-grassed woodland of *Brachystegia spiciformis* Benth. and *Isoberlinia globiflora* Hutch. ex Greenw.; various kinds of thorny *Acacia* woodland, especially *A. rovumae* Oliv.; more or less treeless, grassy valleys dissecting the woodlands; and scattered patches of cultivation often engulfed in tsetse-infested bush. Sleeping sickness (*Trypanosoma rhodesiense* Stephens and Fantham) has broken out in both fly belts in recent years, with a serious epidemic near Kondoa.

2. The Eastern Belt.

I have already explained (1933) why I think that, at some time early in this century, this belt originated from a colony of flies formed from stragglers crossing the high country between the Masai Steppe and the Bubu river. I have described its subsequent progress up to 1932, and forecast the lines along which I expected it to continue. As will be seen, the forecasts were right as far as they went, but they did not cover all the salients since thrust out.

In 1934 Dr. G. Maclean, Sleeping Sickness Officer, caused a survey to be made of the settled areas of Singida ; this brought to light the fact that the eastern fly belt had advanced right into the floor of the Rift Valley. It was then decided to try to prevent the flies ascending the Rift Wall, and to consolidate into a single wide band a line of settlements already existing in the valley below. But while (1935) the clearings were being made to receive the new settlers, the flies passed the proposed barrier (E. Burtt, reports to the Medical Department), and also an emergency barrier formed part-way up the Rift Wall behind it (B. D. and E. Burtt, Departmental Reports). By 1936 they were firmly established on top of the Rift Wall, and by 1938 or 1939 (J. S. Scott, Medical Department) odd flies were being taken above the Rift as far west as the south-eastern tip of the main Turu cultivation steppe (see map).

The fly belt extended rapidly southward down the Rift Valley, as far as the point where the Mponde river plunges into the great Sanzawa thicket ; from there it seemed to be still advancing south-eastward into some uninfested *Brachystegia* woodland in 1938 (R. K. J. Gascoigne, Departmental Report).

All this had been foreseen ; but in southern Kondoa the flies unexpectedly penetrated the very dense *Acacia* woodland in the Bubu and Mekenke valleys, which had apparently halted them from 1928 to 1932. In 1935 (E. Burtt) they had advanced up the Cherai and Kerema rivers as far as the main road running south from Kondoa to Dodoma, and by 1942 (Jackson) they were already across this road, but not much further progress had been made by 1946 (A. G. H. Du Frayer, Departmental Report), and barrier clearings have since been made by the Tanganyika Tsetse Survey and Reclamation Department.

At some time, probably in the late 1930's, the flies also crossed the northern part of the Rift Valley near Lake Balangida Lalu (see map) and established themselves on the Rift Wall directly east of Singida town. This was quite unexpected, because the Rift Wall here is of poor, stunted *Brachystegia* woodland (*B. microphylla* Harms, *B. utilis* Hutch. and Burtt Davy, and *B. spiciformis* Benth.) rising to over 6000 ft.

Finally, the fly belt also broke out unexpectedly northwards towards Hanang. Leaving the *Brachystegia* altogether, the flies struck out across the rolling plains north-east of Balangida Lalu (see map), and by 1942 (Jackson) the advanced spearhead was 8 miles north of the 1928 boundary. They were found established at about 5000 ft. in almost unthicketed small-tree savannah of *Commiphora schimperi* Engl., with grass mainly, *Themeda triandra* Forsk., growing 2 or 3 ft. high, and a very large population of wildebeest (*Gorgon taurinus* Burchell) and other plains game. There seems also to have been some further encroachment to the south-east of Hanang (see map), though here I am less sure that the 1928 boundary shown is correct.

The main lessons to be learned from these advances is that *G. morsitans* is not so dependent on *Brachystegia-Isoberlinia* woodland as had been supposed, and that it can live in either dense *Acacia rovumae* woodland or even small-tree savannah of highly deciduous *Commiphora schimperi* provided game animals are very numerous.

3. The Western Belt.

In 1926 B. D. Burtt observed that *G. morsitans* had passed northward between the main mass of the great Itigi thicket on the right hand and the open grassland of the Wembere on the left, and that it was expanding into a wide area of *Brachystegia* woodland giving it a clear run towards Singida. His 1927 fly boundary is indicated on the map; it encloses a greater width of infested country than that shown by Swynnerton (1936).

Mr. H. Ruhl, formerly for many years Stock Inspector, Singida, who has an intimate knowledge of western Singida, gained partly from his routine duties and partly from elephant hunting, has furnished me with particulars of the dates of first arrival of tsetse in specific places, supporting the idea of a steady advance; but our next information on the western fly front as a whole is from a survey by myself in May–June, 1934. The boundary, presumably for lack of large thicket blocks, open plains, escarpments or other obstacles in the monotonous landscape of south-western Singida, appears as an even bulge (see map) from the debouchement of the Mwaru river in the west to the contact with the Itigi thicket in the east, near the boundary of the main Turu cultivation steppe.

From 1935 there was a good deal of activity north of this fly front, in an attempt to form a two-mile-wide band of defensive settlements westwards as far as the Wembere Steppe, but in the west progress continued rapidly, and already in 1938 (see map) the flies had penetrated far into the *Acacia rovumae* woodland on the edge of the Wembere (R. K. J. Gascoigne, Departmental Report), and were in contact with the barrier clearing. By 1944 (C. Dekker, Departmental Report) they had jumped the clearing at a place called Asasi (not shown on the map), and since then there is information from the District Commissioner that flies had crossed the defensive line of settlements rather nearer to Singida, about where "1944" is printed on the map.

In 1938 or 1939 Mr. J. S. Scott took a fly near the tip of the Turu cultivation steppe, and as it probably came from the western belt I have extended the boundary on the map to enclose this fly. It is in any case evident that the eastern and western belts had virtually coalesced by 1939, as forecast by me in 1933. The matter is of some scientific interest, because the flies from the Kondoa belt are distinguished from those of the great western *morsitans* fly belt as being paler, with paler wings, yellower ground colour on the abdomen and more space in the middle line between the dark bands, which are less defined in the middle than in the western race. Further, the two races remain distinguishable to-day (June, 1949) on the two sides of the point of junction. Thus flies from 5° 10′ S., 34° 32′ E. (see map) are of the dark race, and flies from 5° 5′S., 35° 5′ E. are of the pale race; 12 out of 13 people were able to distinguish correctly two random collections from these two places. There is no doubt that the Kondoa belt, the eastern of the two discussed

here, arose from the great western fly belt in the past, and not from the great eastern belt extending down the coast. (Vanderplank, 1948, notes that the Kondoa flies usually give sterile crosses with those from the great eastern belt.) The paler colour of flies in the Kondoa belt must therefore have appeared after it was separated from the western belt, which supports the theory (1933) that the separation now ended has been long.

4. The Southern Belt.

On the map I have indicated, at the south end of the 35th meridian, a third advance of *G. morsitans*. But in fact it appears that from 1932 (B. D. Burtt) to 1938 (R. K. J. Gascoigne) this fly belt had made no further progress, because it had already reached the end of its area of *Brachystegia* woodland and was circumscribed by a massive block of Itigi thicket.

5. Summary.

1. Two belts of *Glossina morsitans* have for some years past been approaching Singida in Central Tanganyika from east and west, and they have now met at the southern tip of the main Singida cultivated area.

2. The eastern belt has generally done what was expected ; but in addition it has traversed a wide area of dense thorn woodland in the south-east which was supposed to be a barrier ; and in the north has initiated a colony of flies in highly-deciduous small-tree savannah practically without thickets, in the presence of a large population of game animals.

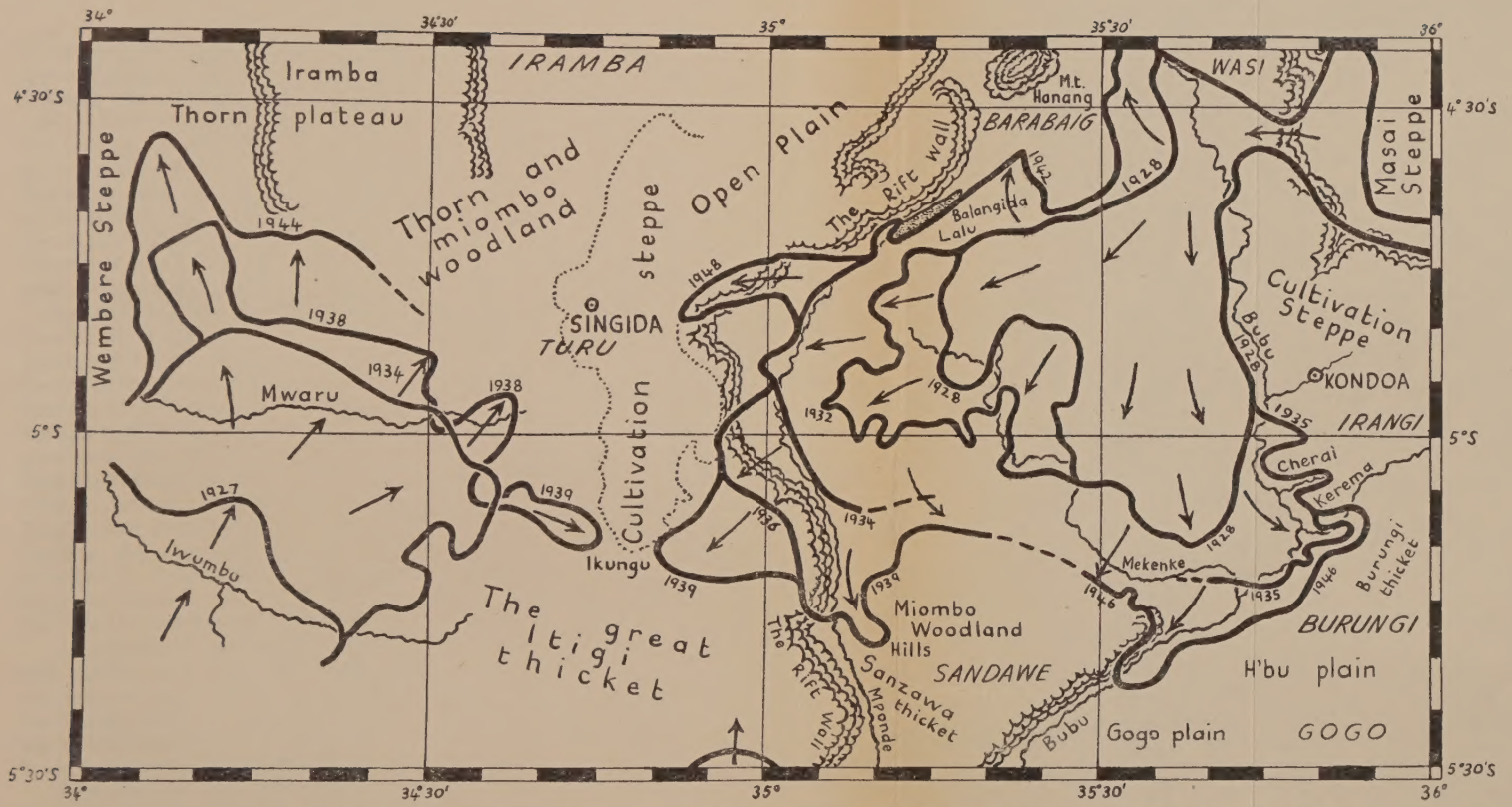
3. The western belt has had fewer natural obstacles, but has jumped a settled barrier intended to arrest its progress, and has gone forward particularly in the thorn woodland bordering the Wembere Steppe.

4. A third advance, from the south, has apparently been stopped by dense thicket.

5. The eastern belt quite certainly arose in the past from the western belt, but flies then receded in both directions and left something like a 200-mile gap between the two. This separation has evidently been long, because the eastern belt has meanwhile become differentiated as a paler race.

References.

Jackson, C. H. N., 1933, *Trans. R. ent. Soc. Lond.* **81** : 205.
Swynnerton, C. F. M., 1936, *ibid.* **84**.



The advances of *Glossina morsitans* in Kondoa and Singida districts of Central Tanganyika. (The names of tribes are in italics.) Scale 1 : 1,000,000.

SPERMATOPHORE PRODUCTION IN *GALLERIA MELLONELLA* L. (LEPIDOPTERA).

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Introduction.

It has long been known that copulation in Lepidoptera occurs by means of spermatophores. Stein (1847) realized that a spermatophore was a case enclosing the semen to be transferred from the male to the female. Petersen (1907, 1909) described a great number of spermatophores from butterflies, and came to the conclusion that they were of considerable importance from a phylogenetic point of view. Klatt (1920) described the sexual organs of *Lymantria dispar* L. and gave an account on the production of the spermatophore in that insect. Michael (1923) and Omura (1938) studied the genital organs of *Bombyx mori* L. and the formation of its spermatophore. The latter mentioned that in addition to the formation of spermatophore the accessory glands of the male moth were responsible for the secretion of what is called the "spermatophragma," i.e. the fluid which hardens and blocks the copulatory opening after copulation. The production of "spermatophragmen" or the sphragidal fluid has been recorded in several other Lepidoptera, namely, most species of *Acraea* and *Parnassius* (Marshall, 1901, and Eltringham, 1925). The function of protecting the impregnated female from other males and so preventing copulation for a second time has been ascribed to the sphragis. This possibility has, however, been regarded with doubt, since the sphragis had been duplicated on several occasions (Michael, 1923, in *Bombyx*, and Eltringham, 1916, in *Acraea*). Moreover, "spermatophragma" has been known to occur in Locustidae. Boldyrev (1913) suggests that it serves to block the female genital opening, and eventually prevents the sperm from coming out. There is no satisfactory evidence for his deduction and the point needs further investigation. In *Galleria* the "spermatophragma" does not occur and the sperm never fail to find the way to the receptaculum seminis.

An account of spermatophore formation as it occurs in *Plodia interpunctella* Hübner was given by Norris (1932). Williams (1939, 1941) gave an extensive survey on the morphology of spermatophores in Lepidoptera; in the bursae copulatrix of many insects he found several spermatophores indicating that copulation was repeated several times. In the present work up to 7 spermatophores have been found in the bursa of *Galleria*.

From the vast amount of literature on Lepidoptera, it is evident that spermatophores are of widespread occurrence among moths and butterflies, and may be the only method of copulation in lepidopterous insects possessing a separate copulatory opening leading to a bursa copulatrix. There is no record as to the formation of spermatophores in other primitive forms which have one genital opening serving for copulation as well as oviposition, i.e. Hepialidae, Micropterygidae, Adelidae, etc.

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Galleria can easily be reared in the laboratory. A culture was kept in an incubator at 30° C. with relative humidity ranging between 70 per cent. and 80 per cent. Although pupae can be differentiated as to sex, it was felt desirable, instead of putting a number of male and female pupae in separate jars (the method of Needham *et al.*, 1937), to place every pupa in a phial with a piece of cottonwool at the bottom and covered by muslin. So virgin females and uncopulated males were obtained, and a pair of known age could be put in a tube, where mating was executed, and observed under the binocular microscope.

The Structure of the Spermatophore.

The lepidopterous spermatophore is formed during the time of copulation. It takes its shape and consistency in the female bursa copulatrix. All spermatophores are built up on a general scheme, and are composed of two parts—a round or oval sac, the body of the spermatophore, and a neck (the Collum of Petersen, 1907). The sac fits in the cavity of the bursa ; the neck is a narrow tube and lies either straight in the ductus bursa, e.g. *Galleria*, or is twisted so that it is bent up beside the body of the spermatophore, e.g. *Ephestia kühniella* Zeller. The opening of the spermatophore usually lies at the tip of its neck. Nevertheless, many of the spermatophores of butterflies have their openings at varying points along their necks. Thus a functionless part, which lies between the opening of the spermatophore and the end of the neck, is blocked. In the female genital tract the opening of the spermatophore lies at the point where the *ductus seminalis* comes off the *ductus bursae* (fig. 4, *a*). In higher Lepidoptera the *ductus seminalis* takes its origin from the body of the bursa itself, or at the junction between the bursa and the *ductus bursae*. In this case the neck of the spermatophore is either twisted up beside the body of the spermatophore, e.g. *Ephestia* and *Plodia*, or reduced in length, e.g. *Bombyx*.

When a spermatophore is recently deposited in the bursa of the wax moth a third part can be distinguished. This is a transparent pearly yellow mass of undefined shape, at the top of the sperm sac (fig. 1, *t.y.m.*). It dissolves easily in water as well as in the secretion of the bursa. So if the bursa of a copulated female is examined 1–2 days after copulation, this mass will be found to have dissolved and only the tough parts of the spermatophore, i.e. the sac and the neck, remain.

The sac is about 1 mm. long and 0·5 mm. wide in the front end, which is the widest part. It is oval in shape, tapering towards the hind end to form a neck. The neck is about 0·84 mm. in length and has an opening at the posterior end, which is about 0·05 mm. in diameter. These dimensions are subject to great variations and small spermatophores were sometimes found. The reduction in size is due, as will be mentioned later, to the small amount of secretion found in the male accessory glands at the time of copulation.

In sections the wall of the sperm sac appears to be formed of two layers, a thick outer cover and a thin inner membrane (fig. 4, *b*, *o.l.* and *i.l.*). The outer cover is lamellated and tends to become thicker at the posterior end of the sac, where it reaches 0·05 mm. in thickness. The semen is enclosed inside the sperm sac. It comprises three elements : the sperm ; a fine granular secretion which accompanies the sperm in the vesiculae seminales ; and another secretion of larger granules derived from the male paired accessory glands. Shortly after copulation the majority of sperm are in the form of

loose bundles ; some, however, are free. A bundle (fig. 2, *c*) comprises a great number of sperm whose heads are closely held together while their tails are free. In the sperm sac the sperm become active shortly after copulation, so that the bundles are broken. The moving sperm can be seen through the wall of the sperm sac if it is dissected out and examined between a slide and a coverslip. In Ringer solution the sperm and the associated substances leave the sperm sac through its opening, and the sperm retain their active movement for a time. The fine granules of the seminal fluid show the Brownian movement, but the large granular secretion seems to form lumps.

The spermatophore has a shining silvery appearance and does not change its colour during the 2 or 3 days following copulation. The spermatophore of the wax moth does not contain any chitin—it dissolves in a saturated solution of caustic potash. A brick-red colour is obtained when it is warmed in a few drops of Millon's reagent. It gives a positive result with xanthoproteic reaction and when boiled for one minute in a few drops of 0·2 per cent. ninhydrin solution a violet colour is developed. Therefore, it is almost certainly composed of protein.

The Spermatophore-producing Organs.

It is well established that the male accessory glands are the source of spermatophores, as is proved by dissecting a pair soon after copulation when the accessory glands will be found to have discharged all their contents and a spermatophore to have developed in the female bursa copulatrix.

The paired vasa deferentia arise from the base of the testes (fig. 2, *v.d.*). Each vas deferens is dilated at the middle, and the two dilatations are always full of sperm and perform rhythmic contractions. The vasa deferentia open posteriorly into a pair of wide ducts and the two points of junction (fig. 2, *v.s.*) are considered by many authors to be the vesiculae seminales (Stitz, 1901 ; Mehta, 1933 ; and Imms, 1934). When males were dissected soon after copulation the two swollen parts of the vasa deferentia were found to be still full of sperm while the vesiculae seminales were empty. Later, these are filled with the motionless sperm conveyed from the testes by means of continuous contractions of the swollen parts of the vasa deferentia. Norris (1932), however, considered that the two dilatations of the vasa deferentia in *Ephestia* were the vesiculae seminales.

The vesiculae seminales receive the paired accessory glands at one end (fig. 2, *p.a.g.*) and the common unpaired gland which terminates in the ejaculatory duct at the other. The unpaired gland is composed of six segments which vary in length and marked with conspicuous constrictions. There is no anatomical difference between these parts, save that the cells towards the ejaculatory duct tend to become longer. The glandular apparatus is devoid of a cuticular intima and is surrounded by a very thin layer of circular muscle.

The unpaired gland comprises two distinct parts. The upper part (*u.p.u.g.*) is nearly two-thirds of the whole length and contains a tough white secretion which clots when it exudes into water. The lower part (*l.p.u.g.*) comprises two segments and contains a transparent yellow secretion which dissolves in water. It was quite common to find the secretion of the upper part invading that of the lower part, so that the white secretion extends into the yellow one.

The components of a spermatophore can be distinguished within the male genital tract. The water-soluble yellow secretion of the lower part of the unpaired gland gives rise to the yellow pearly mass at the top of the sperm sac. The tough white secretion of the upper part of the unpaired gland builds up the walls of the sperm sac and the neck. The contents of the sperm sac are derived from the vesiculae seminales and the paired accessory glands. The chemical tests which had been applied to the spermatophore were also carried out on the contents of the male sexual tract and gave similar results. Frozen sections treated with Sudan black gave negative results.

The unpaired gland leads to the ejaculatory duct, but a marked constriction separates them. The ejaculatory duct is highly muscular with a narrow star-shaped lumen. It dilates slightly at the middle of its course, passes and coils through the penis and opens at its funnel-shaped tip. Both the terminal part of the ejaculatory duct and the outer surface of the penis are denticulated.

Female Organs Concerned With Copulation.

The copulatory opening, the ostium bursae, is situated in the membrane between the 7th and 8th sternites. It is guarded by a sclerotized rim and several bristles (fig. 3, *o.b.*). It leads to the ductus bursae, which dilates at the anterior end forming the bursa copulatrix. In the bursa the muscular layer is not uniformly distributed over the whole surface. It is highly developed on the latero-dorsal side where it forms a ring whose fibres run diametrically (fig. 4, *a*, *m.r.*). The bursa is lined with a thin layer of cuticle which is thrown into folds. The folds become differentiated into sharp teeth at the middle of the muscular ring giving rise to the lamina dentata (fig. 4 *b*, *l.d.*). When a spermatophore is present, the cuticular folds are fully stretched, and the bursa assumes a roundish form.

The bursa is filled with a peculiar secretion. When a bursa is burst in water oily drops float to the surface. Bursae fixed in formalin, embedded in gelatine, cut by the freezing microtome and stained with Sudan black, gave satisfactory evidence that the bursa contained a fatty secretion. The pH, as tested with phenol red and bromo-thymol, was about 7.

The ductus seminalis branches off immediately in front of the ostium bursae (fig. 4 *a*, *d.s.*). This duct leads the sperm to vestibulum where they cross the common oviduct and get into the narrow opening of the ductus receptaculi (*d.r.*). In several cases varying numbers of eggs were found in the ductus seminalis; a phenomenon which has been recorded on several occasions (Norris, 1932, in *Ephestia* and *Plodia*; Stitz, 1901, in *Hydrocampa nymphaeata* L., and Petersen, 1900, in *Pempelia adornatella* T.).

The ductus receptaculi leads to the receptaculum seminis (fig. 4, *a*, *r.s.*) which is provided with a long filamentous gland. The latter is distended at its proximal end forming a reservoir, the lagina receptaculi (*l.r.*). The sperm are stored both in the receptaculum and in the lagina. The lumen of the ductus receptaculi turns round twice in a spiral before opening into the receptaculum (fig. 4, *c*). At the middle of its course the lumen of the duct widens and a cuticular valve is present (*vl.*). Such a structure was found by Eidmann (1929) in other species and named "the inner apparatus." When a female was dissected in saline solution during oviposition the sperm were observed moving actively in the receptaculum and the lagina. The heads of a number of sperm

were found to be held by the valve against the other side of the tube, and their tails actively moving in the round chamber. The valve, therefore, may be responsible for regulating the passage of sperm to fertilize the eggs.

Copulation.

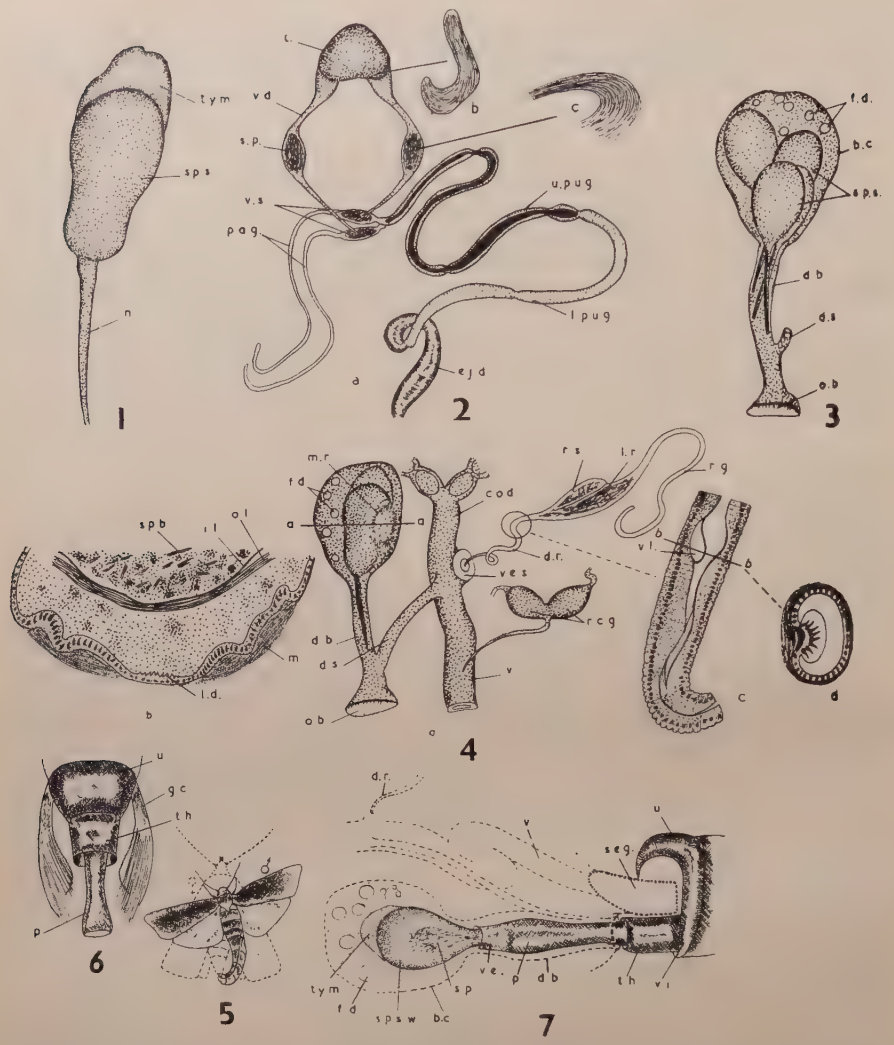
Sex attraction and mating.—The wax moth is sexually mature and eager to mate immediately on issuing from the pupal cocoon. The males and females take up a characteristic " calling " position, fluttering their wings very quickly. The scent glands are situated on the front wings, as described by Barth (1937). He claimed that as the wings move rapidly particles of the smelling substance spread into the air, the male reacts to the smell of the female by moving quickly in her direction and mounts her back. But sex discrimination seems to be not entirely dependent on the movement of the wings. Preliminary experiments showed, firstly, that males would copulate with females whose wings had been amputated ; secondly, that females would also copulate with males without wings ; and thirdly, that copulation occurred even when both insects had had their wings amputated. It is probable, therefore, that a smell emanates from other parts of the body or other senses might be involved in sex discrimination.

In mounting the female's back the male catches hold of a tuft of thoracic scales with his labial palps, elongates his abdomen, everts the copulatory apparatus and protracts the penis. Then, twisting his abdomen which lies on one side of the female (fig. 5), he inserts the penis into the ostium bursae. In doing so he catches hold of the female's 8th abdominal segment from above with his uncus and from the sides with the two claspers (fig. 6 and 7). When the insertion of the penis is secured and the sexual apparatus of the two are firmly held together, he releases the scales of the thorax and comes to lie on a straight line with the female, assuming " end-to-end " position. The two remain thus until the end of copulation. The ovipositor and the vagina are retracted during copulation (fig. 7, *v.*).

During copulation the secretion of the male accessory glands is poured into the bursa and the spermatophore is built up. A spermatophore is completely formed in about three minutes. The insects then separate paying no further attention to each other. On a few occasions, however, they remained *in copula* for a varying length of time ranging from 20 minutes to more than 4 hours. But generally the time of copulation is short compared with *Ephestia* which takes 3–4 hours, *Plodia* 1–1½ hours (Norris, 1932) and *Bombyx* which takes about one hour (Omura, 1938, and Michael, 1923).

Spermatophore formation.—This process has been followed by dipping the insects in Carnoy's fluid 1 and 2 minutes after the beginning of copulation. This solution served as a fixative and killed the insects before they could separate. The bursa was then dissected out and prepared for sectioning.

The penis, during copulation is thrust to a considerable distance into the ductus bursae. A part of the penetration is effected also by the evaginated terminal part of the ejaculatory duct (the vesica). Thus the intromittent organ is brought forward to the anterior end of the ductus bursae (fig. 7, *p.*). The penis pushes in front of it a certain amount of air which fully distends the bursa. The yellow transparent secretion of the lower part of the unpaired gland flows into the bursa and hardens to form the pearly mass. This is



FIGS. 1–7.—(1) The spermatophore of *Galleria mellonella* L. *n*, neck; *sp.s.*, sperm sac; *t.y.m.*, transparent pearly yellow mass. (2) *a*, The male reproductive system; *b*, a sperm bundle from testis; *c*, a sperm bundle from the swollen part of the vas deferens. *ej.d.*, ejaculatory duct; *l.p.u.g.*, lower part of unpaired gland; *p.a.g.*, paired accessory glands; *s.p.*, swollen part of vas deferens; *t*, testes; *u.p.u.g.*, upper part of unpaired gland; *v.d.*, vas deferens; *v.s.*, vesiculae seminales. (3) Bursa copulatrix with four sperm sacs. *b.c.*, bursa copulatrix; *d.b.*, ductus bursae; *d.s.*, ductus seminalis; *f.d.*, fat droplets; *o.b.*, ostium bursae; *sp.s.*, sperm sacs. (4) *a*, The female reproductive system; *b*, T.S., through the bursa copulatrix at (a—a); *c*, ductus receptaculi; *d*, T.S., at (b—b). *c.o.d.*, common oviduct; *d.r.*, ductus receptaculi; *i.l.*, inner layer; *l.d.*, lamina dentata; *l.r.*, lagina receptaculi; *m*, muscular ring; *o.l.*, outer layer; *r.g.*, receptacular gland; *r.c.g.*, reservoir of cement gland; *r.s.*, receptaculum seminis; *sp.b.*, sperm bundle; *v*, vagina; *ves*, vestibulum; *vl*, valve. For other lettering see fig. 3. (5) A couple in the initial position of mating. (6) Male copulatory apparatus. *g.c.*, genital clasper; *p.*, penis; *th.*, theca; *u.*, uncus. (7) The two copulatory apparatus in the end-to-end position. Female organs are represented by broken lines. *p.*, penis; *seg.*, female 8th segment; *sp.*, sperm starting to flow out; *sp.s.w.*, walls of the sperm sac; *th.*, theca; *t.y.m.*, transparent yellow mass; *u.*, uncus; *v.*, vagina; *vi.*, vinculum. For other lettering see fig. 3.

immediately followed by the tough white secretion of the upper part of the unpaired gland which bulges out of the penis forming a small round mass. Sections through the genital organs at this stage show that the white mass, which eventually produces the outer and the inner walls of the sperm sac, has no clear cavity although its centre is vacuolated.

The neck of the sperm sac is formed of the same material, moulded in the penis and retained there until the sperm sac is filled with sperm and the secretion of the paired glands. The cavity of the sperm sac is acquired when sperm and secretion are ejected. These replace the vacuolated centre and the sperm sac increases in size and takes its final shape. The penis then retracts, leaving the neck of the spermatophore in the ductus bursae and copulation comes to an end.

The sexual capacity of males.—During copulation only one spermatophore is formed. A second spermatophore of normal size can be formed within twelve hours after the first. When a male was dissected soon after copulation the whole genital tract except the two vasa deferentia was found to be almost empty. The vesiculae seminales and the paired glands were again charged with their corresponding material six hours after copulation, while the unpaired accessory gland needed more than ten hours.

The size of a spermatophore is dependent on the amount of secretion in the accessory apparatus. Males which copulated within two or three hours from the first copulation produced very small spermatophores which were in some cases devoid of sperm. Three spermatophores of normal size and charged with the normal amount of sperm and secretion can be formed by a single male.

Repeated copulation with females.—A female is usually inseminated several times, and the number of spermatophores in the bursa gives the number of copulations. Of 15 females examined, 4 had one spermatophore, 3 had 2, 3 had 3, 1 had 4, 1 had 5, 2 had 6 and 1 had 7. The sperm sacs were deposited in the bursa while the necks were lying parallel to each other in the ductus bursae. On four occasions it was observed that the insertion of a second spermatophore caused the neck of the first to be twisted beside the sac in the bursa. Such a twisted spermatophore discharged its contents in the bursa.

The amount of sperm in one spermatophore fills the receptaculum seminis and the vagina. The migration of sperm from the spermatophore to the receptaculum starts soon after copulation and takes 2–3 hours, after which time the female begins to lay eggs. A female that had copulated once finished oviposition before the store of sperm had been exhausted. So an additional amount of sperm resulting from a second or a third copulation would, presumably, not be used for egg-fertilization.

The fate of the spermatophore.

Spermatophores in the bursa of old females are represented only by their necks, for the sperm sacs as well as the yellow masses have disappeared. This process of degeneration has been followed from the time of copulation. The yellow mass dissolves within 1–2 days, while the white sperm sac becomes very soft and loses its silvery coloration 4–6 days after copulation. It is then readily broken into pieces if squeezed between a slide and a coverslip. Five days later, i.e. approximately ten days after copulation, the sperm sac dissolves and disappears. In the bursa of a female inseminated several times, the old

spermatophores were represented only by their necks while the new ones were still intact. The thin elastic wall of the bursa, the compressibility of the empty sperm sacs and the disintegration of the old ones explain how a small bursa can hold seven or even more spermatophores.

The bursae of six virgin females were examined in another way. Fragments of congo red fibrin were inserted into the bursae by means of a needle and a pair of forceps. Although the ovipositor was, in most cases, greatly injured, two of the insects lived for five days. On examining the bursae of four females two days after the operation, the fibrin was found to have been digested and the walls were stained pink. It is most probable, therefore, that the sperm sacs are degenerated in a similar way and that the products are absorbed in the bursa copulatrix.

The destruction of the spermatophore has been recorded by Stitz (1901), and Heberdey (1931) in the bursae of other lepidopterous insects. They presumed that a mechanical breakdown had been effected by the lamina dentata. The function of holding the spermatophore in the bursa, however, was assigned to the same structure by Petersen (1907), Eidmann (1931) and others. In *Galleria* spermatophores which were forced to lie in the ductus bursae, owing to the congestion of the bursa with other spermatophores, held in position without the help of the lamina dentata. Moreover, in *Lymantria* the bursa lacks such structure (Klatt, 1920).

Sperm activity.

The sperm bundles are surrounded by a very thin membrane in the lobules of the testes (fig. 2, *b*). The membrane can be demonstrated by applying Giemsa or Leishmann's stains to sperm from the testes. When the sperm bundles get into the vasa deferentia they lose their membranes and become loose (fig. 2, *c*). They are then transferred to the vesiculae seminales and carried in the spermatophore. Omura (1936) described the sperm bundles in *Bombyx*; he showed that their membranes were cast off in the course of penetrating the membrana basilaris, which he described as a membrane separating the lobules of the testes from the efferent ducts.

Sperm obtained from any part of the male sexual tract are motionless in Ringer solution. Once the spermatophore is deposited in the bursa the sperm become very active and start the journey to the receptaculum seminis. Several attempts were made to find out the source of the activating substance. Guided by the experiments of Omura (1936, 1938), the three different secretions of the male accessory glands, viz. the secretion of the paired glands and the white and yellow secretions of the unpaired glands, were applied on a slide in a drop of Ringer solution to sperm from the vesiculae seminales. In each case ten individuals were dissected in saline solution, the segments of the accessory apparatus to be tested were picked up, placed on a slide and sperm were added. The secretion of the bursa was also examined in the same way. In none of the experiments were the sperm activated. Moreover, the whole genital apparatus of ten males were collected, crushed in a little amount of saline solution and centrifuged; the upper part was tested, but again the sperm did not move. A very dilute solution of fructose was also tested, but the same result was obtained. Thus, although the secretion of the lower part of the unpaired

gland was said to activate the sperm in *Bombyx*, similar results could not be obtained in *Galleria*.

As previously mentioned, the contents of the male sexual tract are mostly protein ; yet when a bursa containing a spermatophore was examined for the presence of fat, the blue colour obtained with Sudan black appeared inside as well as outside the sperm sac. The blue colour lined the walls of a recently deposited sperm sac. So it is very likely that the contents of the bursa penetrate the walls of the sperm sac, dissolving in its contents and so activating the sperm.

Summary.

The spermatophore of *Galleria mellonella* L. is composed of three parts : A pearly yellow mass, a sac and a neck. The sac contains the sperm bundles, the seminal fluid which is secreted by the walls of the vasa deferentia, and the secretion of the paired glands.

The spermatophore is built up of the secretion of the male accessory glands, which is mostly protein. The unpaired gland is divisible into two major parts —the upper large part secretes the material for building the walls and neck of the sperm sac, and the lower part produces the secretion which forms the yellow mass.

The spermatophore is received in the female bursa copulatrix. The latter contains a fatty secretion which is probably responsible for activating the sperm in the sperm sac.

In the bursa the yellow mass and the sperm sac are digested and absorbed. The bursa is also capable of digesting bits of fibrin.

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STUDIES ON THE EGGS OF CERTAIN BITING MIDGES (*CULICOIDES* LATREILLE) OCCURRING IN SCOTLAND.

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Introduction.

Before the recent investigation of Hill (1947), in which eggs of *Culicoides impunctatus* Goetghebuer, *C. obsoletus* Meigen, and *C. odibilis* Austen were studied, the only records of the eggs of British species of *Culicoides* appear to have been those of Jobling, 1928 (*C. vexans* Staeger), Steward, 1933 (*C. nubeculosus* Meigen) and Mayer, 1934 (*C. circumscriptus* Kieffer). Observations on eggs of various non-British *Culicoides* were made by Carter, Ingram and Macfie (1920), Patel (1921), Sharp (1928), Dove, Hall and Hull (1932), and Atchley and Hull (1936).

In the present investigation, eggs of *C. fascipennis* Staeger, *C. grisescens* Edwards, *C. halophilus* Kieffer, *C. heliophilus* Edwards, *C. maritimus* Kieffer, *C. impunctatus* Goetghebuer, *C. obsoletus* group (see later), *C. pallidicornis* Kieffer, *C. pulicaris* L., and *C. pulicaris* var. *punctatus* Meigen were obtained. Observations were made on eggs of these species kept moist and at ordinary laboratory or outdoor temperatures, and on eggs exposed to a dry atmosphere and above normal temperatures.

Material and Methods.

Most females used for obtaining eggs were captured, either in the University grounds, Glasgow, or at Rossdhu, on the west banks of Loch Lomond. Species which did not occur in these localities were obtained at Auchterawe, Inverness-shire (*C. grisescens*) or at Arrochar, Dumbartonshire (*C. halophilus* and *C. maritimus*).

For identification, midges were anaesthetised and examined under a binocular microscope. In the main, the nomenclature adopted is that of Edwards (1939), but four species—*C. obsoletus* Meigen, *C. chiopterus* Meigen and two unnamed species (Downes, unpublished data)—could be distinguished only in the male, and will therefore be collectively referred to as the *C. obsoletus* group. Typical *C. pulicaris* and *C. pulicaris* var. *punctatus* could readily be distinguished in the female, and were treated separately in all experiments. In presenting results, however, the two varieties will sometimes be collectively described as being of the *C. pulicaris* group.

It seems generally agreed that a blood meal is a necessary preliminary to egg-laying in *Culicoides* (Patel, 1921; Sharp, 1928; Dove, Hall and Hull, 1932; Atchley and Hull, 1936). Except when obviously gravid at the time of capture, therefore, females to be used for supplying eggs were allowed to feed, either on the arm of the collector, or, more usually, on the ear of a lop-

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eared rabbit, as recommended by Hill (1947). As a rule, single fed or gravid females were placed in 3 × 1 in. tubes; sometimes several were put together in a jar. The bottom of both types of receptacle was covered with several layers of filter paper moistened by periodic watering; a layer of plaster of Paris beneath the filter paper helped to retain the moisture. Eggs were laid on the damp filter paper, which also kept the humidity at the high level necessary for the maintenance of live midges. Carbohydrate food was provided in the form of a raisin or small piece of prune. Laboratory temperature was 13–23° C.

The average length of life of females of most species living under these conditions was 9–11 days, but *C. obsoletus* group females were exceptional in living for an average of 3 weeks, one individual surviving for 3½ months. Eggs were usually laid 1–2 weeks after the blood meal, but the interval varied greatly, even within a species. Females obviously gravid when captured usually laid within a few days. Death usually followed a few days after oviposition, but *C. obsoletus* group females were again exceptional in surviving for an average of 5½ weeks. (Hill, 1947, found that *C. obsoletus* group females always died immediately after laying; since the group is a composite one it is possible we were dealing with different species.) One *C. pulicaris* female and two *C. obsoletus* group females accepted second blood meals after oviposition, and all laid second egg batches.

Breeding receptacles were examined daily, and any filter paper on which eggs were deposited removed. Egg batches were usually divided into several groups. One group was always kept moist and at ordinary laboratory temperatures. Sometimes another group, also moist, was kept in a shaded outdoor area. These two groups will be spoken of as untreated eggs. Often a third group was subjected to some special treatment to be described later. All groups were examined at regular intervals.

Observations on Untreated Eggs.

Culicoides eggs, as laid, were scattered irregularly over the damp filter paper. Usually they are laid singly, sometimes in small clusters. The average number of eggs per batch laid by *C. pulicaris* group females was 93; the average for other species was smaller and varied from 30 to 55.

All eggs obtained were cigar-shaped, grey when newly laid, later some shade of brown. Hill (1947) describes the egg of *C. impunctatus* as being covered with small sucker-like structures arranged in longitudinal rows, and structures of this nature, arranged roughly into longitudinal rows, have been observed on the eggs of all species investigated. There were certain specific differences: in *C. pallidicornis* the longitudinal tracts were particularly well defined; in the *C. obsoletus* group little longitudinal arrangement was apparent. The sucker-like structures of *C. grisescens* eggs seemed smaller than those of other species. With these exceptions, no well defined specific differences in the sculpturing of the chorion were evident. Hill's statement that the stalks of the sucker-like structures of *C. obsoletus* eggs are longer than are those of *C. impunctatus*, sometimes being equal to half the width of the egg, has not been confirmed; as was noted in another context, the divergence between our results may be due to the composite nature of the *C. obsoletus* group. There was a clear-cut difference between the size of the largest eggs obtained (*C. grisescens*: mean

length 0·54 mm.; mean width 0·07 mm.) and the smallest (*C. pallidicornis*: 0·32 mm.; 0·05 mm.), but the size ranges of all other species overlapped greatly.

Hill describes the hatching of *C. impunctatus* eggs in the following words: "A small circular cap splits off at the anterior end of the egg, and simultaneously a longitudinal split occurs antero-posteriorly along the dorsal side for approximately a quarter the length of the egg. This longitudinal split turns sharply to right or to left at its posterior end." Eggs of *C. impunctatus*, and also of *C. fascipennis*, *C. grisescens*, *C. halophilus*, *C. pallidicornis* and the *C. pulicaris* group, examined after hatching, conformed to this description. Of *C. obsoletus* group eggs, which behaved rather differently, Hill states: "A very small cap splits off, and simultaneously a longitudinal split occurs antero-posteriorly; this split may extend almost the whole length of the dorsal side of the egg, although the exact length of the split varies considerably, even in the same batch of eggs." All *C. obsoletus* group eggs examined after hatching conformed to this description.

The duration of the egg stage in the various species of *Culicoides* investigated is shown in Table I. Only four of the comparatively large numbers of

TABLE I.—*The Duration of the Egg Stage in various Species of* Culicoides.

Species.	Date laid.	Date hatching commenced.	Mean duration of egg stage. (days).	Mean laboratory temperature.
C. fascipennis	8. vii.48	14. vii.48	7	18° C.
	9. vii.48	15. vii.48	6	18° C.
C. halophilus	19. vii.47	24. vii.47	5	19° C.
	25. vii.47	1. viii.47	6	19° C.
C. impunctatus	20. vi.48	28. vi.48	9	20° C.
	3. viii.47	12. viii.47	7	21° C.
	8. viii.48	15. viii.48	8	19° C.
C. obsoletus group	18. v.47	20. v.47	2	19° C.
	5. vi.48	7. vi.48	2	19° C.
	18. ix.47	19. ix.47	2	16° C.
	22. ix.47	25. ix.47	3	15° C.
C. pallidicornis	31. vii.47	4. viii.47	4	20° C.
C. pulicaris	11. v.48	16. v.48	5	19° C.
	15. v.48	20. v.48	6	19° C.
	9. ix.47	15. ix.47	6	18° C.
	19. ix.47	26. ix.47	8	16° C.
C. pulicaris var. *punctatus*	2. vi.48	7. vi.48	6	17° C.
	5. vi.48	11. vi.48	6	17° C.
	4. vii.48	9. vii.48	5	18° C.
	5. vii.48	10. vii.48	5	18° C.
C. grisescens	28. ix.46	26.iv.47–3 .v.47	210–217	?
	28. ix.46	10. v.47–17.v.47	216–223	?
	29. ix.46	3. v.47–10.v.47	205–212	?

egg batches obtained from *C. obsoletus* and *C. pulicaris* group females have been entered in this table, these being, in each case, the first two and last two obtained during the adult season. For other species, the data shown are complete. Excepting *C. grisescens* eggs, batches were observed daily and the number of hatched eggs counted; from these data the mean duration of the egg stage in each batch (i.e. the average number of days between laying and

hatching) has been estimated. Since observations, both on the time of hatching, and of laying, were made only once per day, this may, in fact, have been up to one day more or less than the period stated. *C. grisescens* eggs were observed at weekly intervals ; the duration of the egg stage is therefore given only to within seven days. The mean laboratory temperatures cited are based on daily maximum and minimum readings.

It will be noticed that the egg stage of *C. grisescens* was of several months duration ; eggs obtained in September hatched in April or May. Other species, which hatched a few days after laying, differed in some degree among themselves : *C. obsoletus* group eggs consistently developed more rapidly than those of other species, and, allowing for temperature differences, *C. impunctatus* eggs were consistently slowest. Further distinctions do not seem warranted by the data available.

Judging from daily maximum and minimum readings, mean outdoor shade temperatures were always lower than mean laboratory temperatures, and eggs kept out of doors normally hatched a few days later than those in the laboratory. Here, again, *C. grisescens* eggs were exceptional. Although under observation at a time when the outdoor-indoor temperature difference was wide, eggs of this species kept outside hatched in February, 2–3 months earlier than did eggs from the same batches kept in the laboratory.

The proportion of eggs which hatched in any given batch was usually approximately 75 per cent. Sometimes none at all hatched. Eggs failing to hatch usually contained dense embryonic tissue indistinguishable from the contents of normal eggs, and sometimes an apparently fully developed larva was visible within the egg. At other times eggs remaining unhatched were unusually pale in colour, in which case they frequently lacked the dense contents of normal eggs. Possibly some artificiality in the laboratory environment acting, either directly on the egg, or indirectly through the parent, was responsible for the high mortality sometimes experienced.

Experiments on the Viability of the Eggs.

The viability of *Culicoides* eggs under certain conditions was tested by exposing them to a dry atmosphere—this, for brevity, will be referred to as " drying "—and to temperatures of 30° C. or 35° C. for varying periods. Apart from the *C. obsoletus* group, which had the drawback of comprising several largely indistinguishable species, the only eggs available in fairly large numbers were those of *C. pulicaris* and *C. pulicaris-punctatus*. Most experiments were therefore performed on these two varieties. Egg batches were subdivided into groups of 20. One group from each batch was always kept moist and at normal room temperature (i.e control group) ; the other groups were treated in the ways described below. The serial number of the batch from which each egg group was taken is included in all tables showing the results of the experiments. As before, observations on the number of eggs hatched were made daily ; the actual duration of the egg stage may therefore have been up to one day more or less than the time stated.

The drying procedure was to place the area of damp filter paper bearing the eggs on a larger piece of dry filter paper inside a calcium chloride desiccator, the duration of treatment being timed from half an hour after this to the time when the eggs were remoistened. Tables IIA and IIB show the results of drying

TABLE IIA.—*The Survival of* C. pulicaris *Eggs exposed to a Dry Atmosphere.*

Number of eggs per group = 20

Duration of treatment (hours).	Time between laying and treatment (days).	Number of eggs hatching. Treated (T).	Control (C).	T C 100.	Mean duration of egg stage (days) Treated (T).	Control (C).	T C 100.	Egg batch number.
12	0	0	17	0	.	5	.	8
	1	20	17	117	8	5	160	8
	2	20	17	117	7	5	140	8
	3	18	17	106	6	5	120	8
	4	20	17	117	6	5	120	8
		1	1	100	7	7	100	13
		18	19	95	8	6	133	17
18	0	0	19	0	.	6	.	17
	1	0	19	0	.	6	.	17
	2	0	19	0	.	6	.	17
	3	0	19	0	.	6	.	17
	4	9	19	47	7	6	116	17
24	0	0	17	0	.	5	.	1
		9*	11	(82)	7	8	(88)	25
	1	0	17	0	.	5	.	1
		3*	11	(27)	8	8	(100)	25
	2	0	17	0	.	5	.	1
		0	13	0	.	6	.	6
		0	3	0	.	6	.	7
	3	0	13	0	.	6	.	6
		0	3	0	.	6	.	7
	4	1	20	5	10	6	167	5
		0	3	0	.	6	.	7
		10	11	91	14	8	175	25
48	0	0	16	0	.	5	.	11
	1	0	16	0	.	5	.	20
	2	0	5	0	.	7	.	15
	4	0	16	0	.	5	.	11
		0	16	0	.	5	.	20

* Abnormal hatching (see text).

C. pulicaris group eggs for 12, 18, 24 and 48 hours at various stages of development. They bring out the following points :

(*a*) Most eggs survived 12 hours, some 18 and 24 hours, but none 48 hours' drying.

(*b*) There was a tendency for survival of drying to increase with the age of the eggs when treated. Thus *C. pulicaris* eggs survived 12 hours' drying only when treated one or more days after laying, while 18 and 24 hours' treatment was followed by normal hatching only if the eggs were at least four days old ; the small terminal split of *C. pulicaris* eggs which hatched after 24 hours' treatment at an earlier stage of development was quite distinct from normal hatching. Similarly, *C. pulicaris-punctatus* eggs survived 12 and 24 hours' drying only when treated one or more days after laying. The significance of these results is increased by the fact that some of them are based on the hatching of series of groups derived from the same egg batch. Cases in point are batches 8 (12 hours' drying), 17 (18 hours) and 25 (24 hours) in Table IIA, and batches 4 (12 hours' drying) and 3 (24 hours) in Table IIB ; all except the last showed a tendency for survival of drying to increase with age.

TABLE IIB.—*The Survival of* C. pulicaris *var.* punctatus *eggs exposed to a dry Atmosphere.*

Number of eggs per group = 20.

Duration of treatment (hours).	Time between laying and treatment (days).	Number of eggs hatching. Treated (T).	Control (C).	$\frac{T}{C}$ 100.	Mean duration of egg stage (days). Treated (T).	Control (C).	$\frac{T}{C}$ 100.	Egg batch number.
12	0	0	18	0	.	5	.	4
	1	19	18	106	6	5	120	4
	2	17	18	95	6	5	120	4
	3	18	18	100	6	5	120	4
	4	19	18	106	7	5	140	4
24	0	0	19	0	.	6	.	1
	1	0	19	0	.	6	.	1
		7	15	47	8	6	133	3
	2	0	19	0	.	6	.	1
		4	15	27	7	6	116	3
	3	0	19	0	.	6	.	1
		1	15	7	8	6	133	3
	4	0	19	0	.	6	.	1
		10	19	53	9	6	150	2
	5	12	19	63	8	6	133	2
		8	15	53	8	6	133	3
48	0	0	13	0	.	4	.	5
	2	0	13	0	.	4	.	5
	4	0	8	0	.	5	.	6

(*c*) Drying had the effect of delaying hatching; only once when normal hatching occurred did it take place as early in the treated as in the control group. The duration of the egg stage did not, however, vary consistently, either with the age of the egg when treated, or with the duration of treatment; perhaps more precise data would reveal such relationships.

Eggs to be exposed to above-normal temperatures were kept on moist filter paper inside a closed petri dish, and placed in an incubator at a temperature of either $30 \pm \frac{1}{2}$° C. or $35 \pm \frac{1}{2}$° C. The duration of treatment was timed from half an hour after the eggs were placed in the incubator to the time of removal. The results of treating *C. pulicaris* group eggs in this way are shown in Table III, which brings out the following points:

(*a*) Exposure to 30° C. for 12, 24 and 48 hours, and to 35° C. for 12 hours, was always survived by eggs of both varieties. *C. pulicaris* eggs usually survived 24, but never 48 hours, at 35° C.; *C. pulicaris-punctatus* eggs always survived both 24 and 48 hours at this temperature.

(*b*) The divergent results obtained with exposures at 35° C. seem to indicate that, as far as above-normal temperatures are concerned, at least, *C. pulicaris-punctatus* eggs are more viable than are *C. pulicaris* eggs.

(*c*) The survival of *C. pulicaris* eggs tended to increase with their age when treated. *C. pulicaris-punctatus* eggs showed no consistent relationship of this nature, perhaps because the conditions to which they were exposed were, in most experiments, well below their limit of endurance.

(*d*) Exposure to 30° C. tended to shorten the duration of the egg stage, exposure to 35° C. to lengthen it. The acceleration produced by exposure to 30° C. was more pronounced in *C. pulicaris-punctatus* than in *C. pulicaris*, the retardation produced by 35° C., less so. These results, though requiring con-

firmation, are another indication that *C. pulicaris-punctatus* eggs are less adversely affected by above-normal temperatures than are *C. pulicaris* eggs.

The procedure for exposing eggs simultaneously to a dry atmosphere and a temperature of 30° C. or 35° C. was identical with the drying procedure except that the desiccator was kept inside an incubator at the required temperature.

TABLE III.—*The Survival of* C. pulicaris *Group Eggs exposed to above-normal Temperatures.*

Number of eggs per group = 20.

Species.	Temperature.	Duration of treatment (hours).	Time between laying and treatment (days).	Number of eggs hatching: Treated (T).	Control (C).	T C 100.	Mean duration of egg stage (days): Treated (T)	Control (C)	T C 100.	Egg batch number.
C. pulicaris	30° C.	12	0	8	15	53	6	5	120	9
			2	16	18	89	6	6	100	16
			4	15	15	100	5	5	100	9
		24	0	12	15	80	6	5	120	9
			1	19	19	100	6	6	100	2
			2	18	18	100	5	6	83	16
			4	20	20	100	6	6	100	5
		48	0	1	1	100	4	7	57	13
			3	3	1	300	6	7	86	13
	35° C.	12	0	20	18	109	6	5	120	10
			2	14	18	78	7	6	117	16
			4	20	18	109	6	5	120	10
		24	0	0	18	0	.	5	.	10
			1	1	19	5	9	6	150	2
			2	18	18	100	8	6	133	16
			4	19	18	106	7	6	117	4
		48	0	0	18	0	.	6	.	12
			4	0	18	0	.	6	.	12
C. pulicaris var. *punctatus*	30° C.	24	0	16	8	200	3	5	60	6
			2	20	15	133	5	6	83	3
			4	19	19	100	4	6	67	2
		48	0	15	19	79	3	5	60	8
	35° C.	12	0	19	18	106	4	4	100	7
			4	20	19	105	5	5	100	8
		24	0	19	18	106	4	4	100	7
			2	18	15	120	5	6	83	3
			4	17	19	89	6	6	100	2
		48	0	8	20	40	6	5	120	9
			4	15	19	79	6	5	120	8

Under these conditions the temperature of the eggs presumably rose more rapidly than when they were enclosed in a petri dish, the temperature of which also had to be raised from room level, and the higher temperature probably also increased the rate of drying. The duration of treatment was therefore timed from only 15 minutes after the eggs were placed in the warm desiccator.

As will be seen from Table IV, all groups, with one exception, failed to hatch. Even when hatching began it was not completed; larvae emerged half-way from the egg and then died. From a comparison of these results with those presented in Tables II and III it is evident that drying and an above-normal temperature in combination are more harmful than is either alone. This is not necessarily an indication that exposure to the one condition increases susceptibility to the other; it may be that eggs dried at the higher temperature lost more water than those dried at room temperature.

Although it is, perhaps, unwise to lay emphasis on a single hatching, it may be noted that the results shown in Table IV, so far as they go, are consistent with conclusions reached earlier. Thus the one group which hatched was *C. pulicaris-punctatus*, and it was treated four days after laying; it was suggested earlier that *C. pulicaris-punctatus* is the more viable of the two varieties, and that resistance to unfavourable conditions increases with the age of the egg.

The few experiments performed on eggs of other species gave the following results :

C. impunctatus eggs did not survive 24 hours' exposure to a dry atmosphere when treated 0 and 7 days after laying.

C. obsoletus group eggs—which may have included those of several different species—exposed to 24 and 48 hours' drying 0, 1 and 2 days after laying survived only once, i.e. when dried for 24 hours on the day of laying. There was no survival after a 24-hour exposure to 35° C. 0 and 1 days after laying.

C. grisescens eggs survived all drying treatments to which they were subjected. These were 24 hours' drying 8, 10, 13 and 14 days after laying, and 48 hours' drying 14 days after laying.

TABLE IV.—*The Survival of* C. pulicaris *Group Eggs exposed to a dry Atmosphere together with an above-normal Temperature.*

Number of eggs per group = 20.

Species.	Temperature.	Duration of treatment (hours)	Time between laying and treatment (days).	Number of eggs hatching. Treated (T).	Control (C).	T C 100.	Mean duration of egg stage (days). Treated (T).	Control. (C).	T C 100.	Egg batch number.
C. pulicaris	Drying at 30°C.	12	0	0	20	0	.	5	.	9
			4	0	20	0	.	5	.	9
		24	0	0	19	0	.	6	.	17
			4	0	16	0	.	5	.	11
			0	0	20	0	.	6	.	5
	Drying at 35° C.	12	0	0	18	0	.	5	.	10
			4	0	18	0	.	5	.	10
		24	0	0	18	0	.	5	.	10
			4	0	18	0	.	5	.	10
C. pulicaris var. *punctatus*	Drying at 30° C.	12	0	0	20	0	.	5	.	9
			4	17*	19	(89)	5	5	(100)	8
	Drying at 35° C.	12	0	0	20	0	.	5	.	9
			4	0	19	0	.	5	.	8

* Incomplete hatching (see text)

Apart from the fact that *C. grisescens* eggs seem less affected by exposure to a dry atmosphere than *C. pulicaris* group eggs, these results give no indication that eggs of the species they concern differ markedly in viability from those of the *C. pulicaris* group. The data are, of course, very incomplete, and further experiments might reveal such differences.

The Significance of the Results in Nature.

In prolongation of the egg stage, *C. grisescens* differed from all other species investigated. The only other record of several months elapsing between laying and hatching in *Culicoides* appears to be that of Jobling (1928), who found that eggs of *C. vexans* laid in June hatched in October. Taking into account the times of year at which *C. grisescens* eggs were laid (September), and hatched (February, when kept out of doors), it seems that this species spends much of the colder part of the year in the egg stage.

Other species investigated, it will be recalled, hatched a few days after laying. *C. obsoletus* group and *C. pulicaris* eggs were obtained at all stages of the adult season—i.e. from May to October—and the fact that eggs obtained at the end, like those obtained earlier in the season, hatched within a few days, indicates that these species spend the colder part of the year in the larval stage ; the pupal stage of *C. pulicaris* and the *C. obsoletus* group, like that of other species of *Culicoides*, has been observed to last only a few days. Eggs of other

species investigated were not actually obtained at the ends of their respective adult seasons, but there is no reason to suppose that the duration of their egg stages would have been different had this been so; probably these species also overwinter as larvae. That this is true of *C. impunctatus*, *C. pallidicornis*, and the *C. obsoletus* group is borne out by the observations of Hill (1947) on the life-histories of these species.

The fact that *C. grisescens* eggs exposed to outdoor temperatures hatched two to three months earlier than those exposed to the higher laboratory temperatures is suggestive of a diapause comparable to that of overwintering eggs of the silkworm, *Bombyx mori* (Duclaux, 1869, cited by Wigglesworth, 1947). Silkworm eggs will complete their development and hatch only if they have been exposed to temperatures near freezing point for a certain period. In *C. grisescens*, apparently, exposure to indoor (+ 6° C. to + 21° C.) instead of outdoor (− 2° C. to + 17° C.) temperatures did not prevent development, but merely delayed it.

In any attempt to relate the results of experiments on the viability of *Culicoides* eggs to conditions in nature the difficulty at once encountered is ignorance of the precise microclimatic conditions to which the eggs are normally exposed. The humidity of the microclimate must depend on the amount of moisture in the vicinity, and on the temperature; the temperature depends on the amount of heat absorbed and radiated by the substratum, on its specific heat and conductivity, and on the extent to which complicating conditions such as a high rate of evaporation or bacterial fermentation are operating. Of the species dealt with, *C. pulicaris* group, *C. obsoletus* group and *C. impunctatus* adults, have been reared from a large number of habitats (e.g. waterlogged mud, damp soil, compost heap), the temperature and humidity conditions of which may vary widely, while the breeding place of *C. grisescens* is not known. The following discussion is therefore largely speculative.

So far as is known, *Culicoides* eggs are always laid in fairly moist situations, and in the damp climate of Britain, prolonged drying of their substratum probably very rarely occurs. Even when it does it is highly unlikely that the humidity to which they are exposed is ever as low as that in a calcium chloride desiccator. *Culicoides* eggs of the species investigated, which, as has been shown, may survive 24 or even 48 hours in a desiccator, are therefore seldom likely to suffer a high mortality due to desiccation.

The only available guide to the temperature conditions to which *Culicoides* eggs are exposed in nature, though a highly inadequate one, seems to be air temperature. In Britain, air temperatures almost never rise to 35° C. (95° F.); 30° C. (86° F.) is seldom reached, and is never maintained for as long as 24 hours. It appears, therefore, that the capacity of moist *C. pulicaris* group eggs to survive 48 hours and perhaps longer at 30° C., and 12, sometimes 24 and 48 hours at 35° C., is rarely likely to be brought into play. Simultaneous exposure to drying and above-normal temperatures, judging from the results presented, has a fatal effect within 12 hours; conceivably some mortality due to this occurs during hot dry summer weather.

Summary.

Eggs were obtained from several species of *Culicoides* occurring in Scotland. Most hatched a few days after laying, but *C. grisescens* eggs laid in September

did not hatch until February or later, thus indicating that this species spends much of the colder part of the year in the egg stage.

C. pulicaris group eggs (i.e. eggs of *C. pulicaris* and of *C. pulicaris* var. *punctatus*) exposed to the dry atmosphere of a desiccator usually survived 12 hours, sometimes 18 and 24 hours, but never 48 hours, of such treatment. Survival tended to increase with the age of the eggs when treated. Hatching, when it occurred, was later than in untreated eggs.

C. pulicaris group eggs survived 12, 24 and 48 hours' exposure to 30° C., and 12, sometimes 24 and 48 hours' exposure to 35° C. In this respect *C. pulicaris* var. *punctatus* eggs appeared more viable than *C. pulicaris* eggs. Exposure to 30° C. tended to shorten the duration of the egg stage, exposure to 35° C. to lengthen it.

C. pulicaris group eggs exposed to a dry atmosphere at 30° C. or 35° C. for 12 or 24 hours never survived.

The significance of the results in nature is discussed.

Acknowledgments.

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SPERMATOPHORE PRODUCTION IN *BLATTELLA GERMANICA* L. (ORTHOPTERA : BLATTIDAE).

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Introduction.

The production of spermatophores in Blattidae has been dealt with by very few authors. Zabinski (1933*a*) was the first observer who reported the occurrence of a spermatophore in *Blatta orientalis* L. Qadri (1938) described the same spermatophore but did not deal with its development in any detail. Wille (1920) found no evidence of spermatophore formation in *Blattella germanica* L. and claimed that free sperm were delivered to the female. This wrong statement caused Snodgrass (1937) to express astonishment at the different methods of sperm transference in Blattidae, in spite of the fact that the phallic organs in this family are morphologically almost uniform and all species have highly developed male accessory glands. Wille based his opinion on the examination of one pair soon after a copulation that lasted for six seconds. He took this for a successful copulation, and found no spermatophore.

Gupta (1947), realizing the conflict between Qadri's and Zabinski's views with regard to the development of the spermatophore, tried to clarify the problem in *Periplaneta americana* L. He described the spermatophore in this insect, but gave a misleading account of the process of spermatophore production. He stated "that the rudiments of the spermatophore first appear at the anterior end of the ejaculatory duct, only 20 to 24 hours after the final moult . . . the spermatophore increases in size and slowly descends down the ejaculatory duct till the end of the fifth or sixth day, when it occupies almost half the length of the duct." It has been found that this statement does not apply either to the *Blattella* spermatophore, or to that of *Periplaneta americana* itself. In those insects not possessing a spermatophore mould, a spermatophore is produced only during the process of copulation.

The difficulty in finding spermatophores in cockroaches and in following the different stages of their development can be attributed to the particular conditions under which the insects copulate. They have rarely been seen during the process of copulation, and therefore many authors have missed not only the presence of spermatophores, but also the function of many genital appendages.

The work described in this paper has been undertaken with the object of verifying the opinions of the above-mentioned writers, to find out how far spermatophores do occur in other members of the family and to study the process of spermatophore production in one of the orthopterous insects that has no spermatophore mould (*see* Snodgrass, 1937). The work was very much facilitated by a huge culture of *Blattella germanica* L., kept successfully in the laboratory, from which 20 pairs *in copula* were picked up and dealt with in different ways. Copulation was found to take 2–3 hours during which time

the pair would not separate, even if they were dipped in Carnoy's fluid or anaesthetized for dissecting purposes. Some were examined soon after copulation, while the male accessory glands of others were dissected out and fixed at varying stages during the process and prepared for sectioning or direct examination.

Acknowledgments.

I should like to express my indebtedness to Dr. W. H. Thorpe, who supervised this work, and to Dr. J. S. Kennedy for reading the manuscript.

The Structure of the Spermatophore.

If the subgenital sternum of a female that has just finished copulation is carefully cut away from its basal connection, a spermatophore may be found firmly adhering to a certain set of sclerites of the eighth sternum (fig. 1, *a* and *b*). The spermatophore (fig. 2) is an oval, flattened mass, milky in general

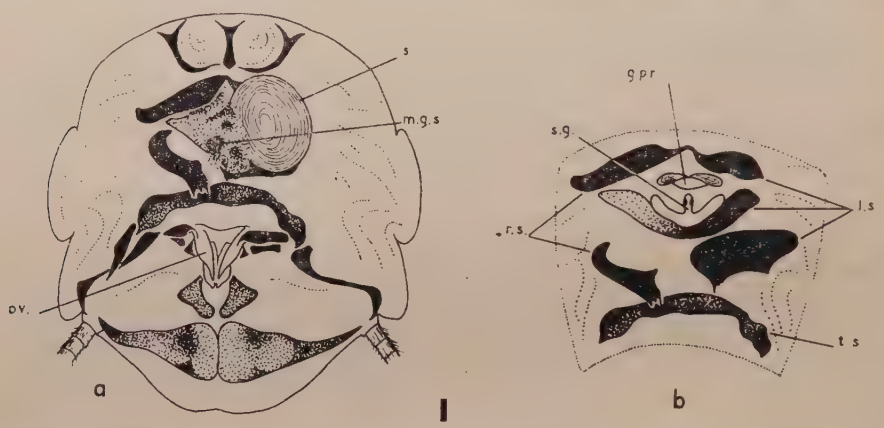

Fig. 1.—(*a*) A general view of the female external genitalia exposed by removal of the seventh sternum after the reception of the spermatophore. (*b*) The genital sclerites of the 8th sternum when the spermatophore is removed. *gpr.*, Gonopore, the opening of the common oviduct; *l.s.*, left genital sclerites; *m.g.s.*, masses of milky granular substance; *ov.*, ovipositor; *r.s.*, right sclerites; *s.*, spermatophore; *s.g.*, spermathecal groove; *t.s.*, transverse sclerite.

appearance and tough in consistency. It is about 2 mm. in length and 1 mm. in width. Its tip, which contains the openings of the sperm sacs, is inserted into the widened spermathecal groove in such a way that the two spermathecal openings come in direct contact with the two openings of the sperm sacs.

Three distinguishable secretions go to make up the body of the spermatophore (fig. 2, *a*). A clear transparent mass (*t.m.*) convering the ventral surface of the spermatophore, a milky white mass (*m.w.m.*) that contains the two sperm sacs, and a translucent lamellated mass (*t.l.m.*) which forms the dorsal wall of the spermatophore and is in close contact with the female sclerites after copulation. A number of masses of a milky granular secretion (fig. 1, *a*, *m.g.s.*) are scattered over the spermatophore and the adjacent sclerites of the female.

The two flattened sperm sacs (fig. 2, *b*, *sp.s.*) lie closely adjacent to one

another, each with a separate duct to the outside. In each cavity the heads of the sperm are arranged in a layer applied to the walls.

At the moment of ejection the spermatophore has an elongate form. Its tip, containing the two openings of the sperm sacs (fig. 2, *a*, *t.*), comes out first and is inserted into the spermathecal groove (fig. 1, *b*, *s.g.*). The body of the spermatophore is then applied to the three sclerites lying on the left-hand side of the spermathecal groove with the transparent mass directed towards the ventral side. The spermatophore is held firmly by these sclerites ; but whether or not a sticky substance is secreted that helps in holding the spermatophore in place, it is very difficult to demonstrate. During copulation the very large evaginated endophallus secures the spermatophore onto the three sclerites and presses it so that it takes a flattened form.

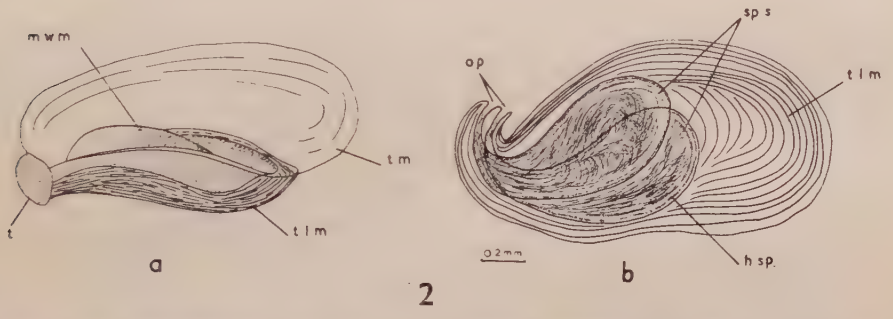

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FIG. 2.—(*a*) Spermatophore, side view. (*b*) A cleared preparation of same. *h.sp.*, Heads of spermatozoa ; *m.w.m.*, milky white mass containing sperm sacs ; *op.*, openings of the sperm sacs ; *sp.s.*, sperm sacs ; *t.*, tip of the spermatophore ; *t.l.m.*, translucent lamellated mass ; *t.m.*, transparent mass.

The spermatophore remains in place for about 12 hours, during which time the sperm migrate to the spermathecae, the spermatophore shrinks and eventually releases itself from the hold of the sclerites, and the masses of milky secretion scattered on the spermatophore and the sclerites dry up. A few hours later the spermatophore is dropped and no sign of copulation can be seen on the female's sclerites.

It was only on one occasion out of twelve that the spermatophore was placed on the right-hand side of the spermathecal groove, held in position by two sclerites (fig. 1, *b*, *r.s.*) ; a front one which is merely an extension of the anterior left sclerite, and a posterior one. It is clear, therefore, that the five sclerites surrounding the opening of the common oviduct and the spermathecal groove, which are part of the eighth sternum, serve for holding the spermatophore.

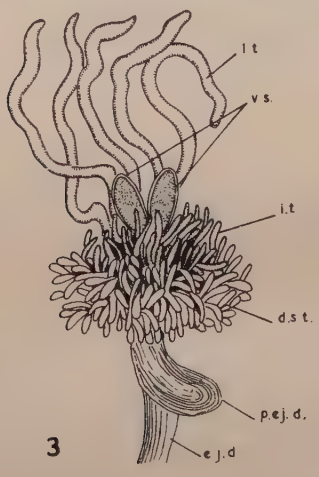
Soon after the separation of a mating couple the two sperm sacs are full of sperm. When a spermatophore is detached carefully at this moment and placed in saline solution the sperm flow out from the tip of the spermatophore and move actively in the solution. In water, however, no sperm come out. This shows that the question of sperm migration in *Blattella* is totally different from that of *Gryllus domesticus*. In the latter the migration of sperm to the spermatheca is carried out by forces provided by the spermatophore ampulla

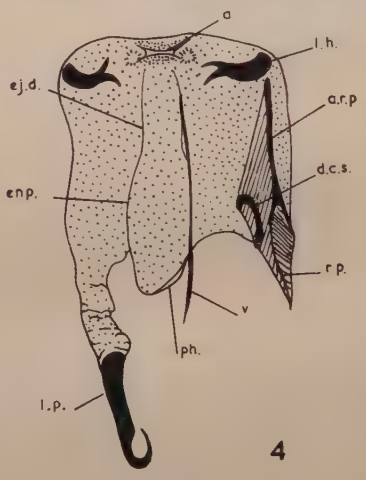
which remains outside the female organs after copulation. In *Blattella*, however, the sperm have to be chemically activated before they can leave the spermatophore. The spermathecae in the female are accompanied by two huge spermathecal glands which are almost certainly responsible for stimulating the sperm in the spermathophore.[1] Such glands are lacking in *Gryllus*.

The transparent mass covering the ventral surface of the spermatophore swells considerably in water and almost disappears within 12 hours. The other parts of the spermatophore also become swollen and much twisted. In Carnoy's fluid the transparent mass quickly disappears and the other parts are apt to shrink. The different parts of the spermatophore are built up of protein and do not contain any chitin.

The Spermatophore-producing Organs.

The male accessory glands of *Blattella germanica* have been figured by Snodgrass (1937). He divided them into two groups according to their length. But according to their contents they can be sorted out into three different groups (fig. 3). A ventral group comprises 4–6 long tubules, containing milky





Figs. 3–4.—(3) Male accessory glands. *d.s.t.*, Dorsal short tubules; *ej.d.*, ejaculatory duct; *i.t.*, intermediate tubules; *l.t.*, long tubules; *p.ej.d.*, pouch of the ejaculatory duct; *v.s.*, vesiculae seminales. (4) Male external genitalia exposed by removal of the tenth tergum. *a.*, Anus; *a.r.p.*, apodeme of right phallomere; *d.c.s.*, dark crescentic sclerite; *ej.d.*, ejaculatory duct; *enp.*, endophallus; *l.h.*, lateral hook; *l.p.*, left phallomere (protracted); *ph.*, phallotreme; *r.p.*, right phallomere; *v.*, virga.

secretion; each is about 4 mm. in length and 0·4 mm. in thickness. The secretion does not stain with haematomylin, but stains readily with picric acid. The most dorsal group comprises a great number of shorter tubules containing a transparent secretion that dissolves easily in water. Each tube is about 1 mm. in length and 0·2 mm. in thickness. The secretion stains with haematoxylin and acquires a weak violet colour. The third set of glands is

[1] A full account of the female internal genital organs can be found in the work of Snodgrass (1937).

found between these two groups. It comprises a great number of tubules surrounding the *vesiculae seminales* from the dorsal and the lateral side. The tubules are about 1·3 mm. in length and 0·2 mm. in thickness. They contain a translucent secretion that takes a blue colour with haematoxylin. The secretion of all types of tubules gives protein-positive reactions.

The walls of these tubules are all built up of the same elements, one layer of glandular cells surrounded by a muscular layer. The wall of the longest type of tubules is very thin, as the cells are considerably stretched.

The accessory glands open into the pouch of the ejaculatory duct. On dissecting any non-copulating male this pouch appears as a more or less collapsed sac that lies in a posterior position to the whole mass of tubules (fig. 3, *p.ej.d.*). During copulation, however, the secretion of the different glands slips into it,

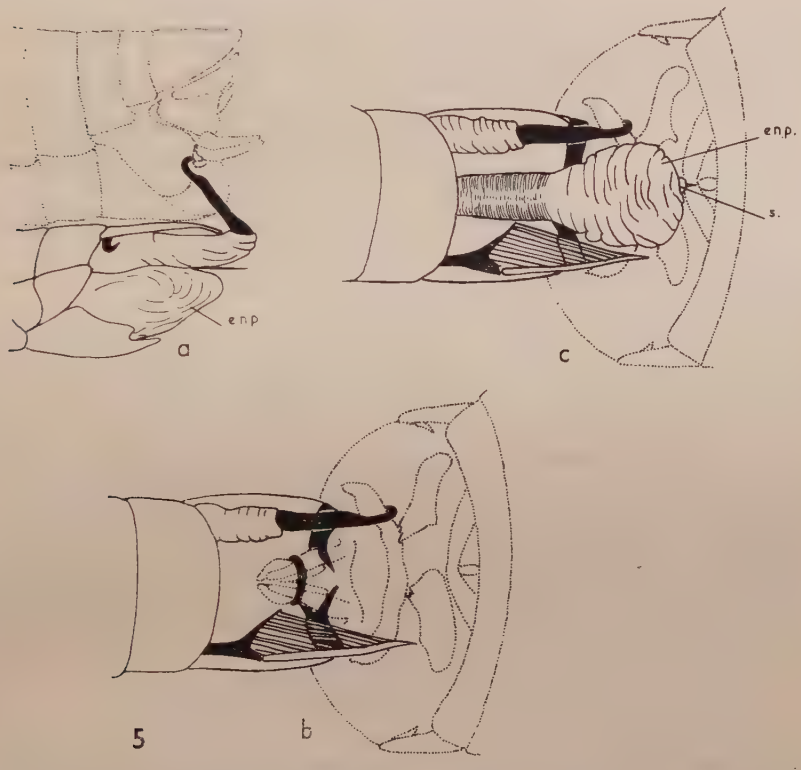


FIG. 5.—Three diagrammatic representations showing the part played by the external genitalia during copulation. The female organs are represented by dotted lines. (*a*) A side view of the initial position. The left phallomere is fully protracted, inserted into the female's genital chamber and holding the transverse sclerite in front of the ovipositor. (*b*) The insects assuming the end-to-end position. The lateral hooks are holding the ovipositor from both sides and the crescentic sclerite is holding it from the ventral side. The last sterna in both insects and the endophallus have been removed. (*c*) The endophallus is much evaginated at the moment the spermatophore is fully developed and ready to be pushed out. The last sterna in both insects have been removed. *enp.*, Endophallus ; *s.*, spermatophore.

and at the final stage, when the spermatophore is almost fully developed,the pouch is fully distended and directed anteriorly. The whole mass of the accessory glands is then on its dorsal side (fig. 6, *c*).

Copulation.

The part played by the dorsal abdominal glands in the sexual behaviour of cockroaches has been dealt with by many authors, such as Gerstaecker (1861), Minchin (1889, 1890), Hasse (1889), Oettinger (1906), Harrison (1906), Sikora (1918), Wille (1920), Koncek (1924), Rau (1924) and Zabinski (1933). It is known that the male cockroach carries the female on his back at the beginning of copulation, and that they soon assume an end-to-end position. Wille's (1920) account of the copulation of *B. germanica* needs, however, further amplification with regard to the part played by the male genital appendages in holding those of the female. The structure of the genital appendages of both sexes has been studied by Snodgrass (1937) ; a simple diagram for the male external genitalia, however, is appended (fig. 4).

As the male slips under the body of the female the hooked left phallomere is fully extended. It is directed upwards and inserted into the female's genital chamber, clasping at the large crescentic sclerite situated in front of the ovipositor (fig. 5, *a*). When it secures a hold on the sclerite the initial position, which lasts for only a few seconds, comes to an end and the couple take up the end-to-end position. It is only now that the male acquires a hold on the ovipositor. In *Blatta orientalis,* Qadri (1938) claimed that the hold on the ovipositor is secured during the initial position.

When the end-to-end position is obtained the two lateral hooks lying on both sides of the male anus move backwards to hold the ovipositor from both sides at a point near its base (fig. 5, *b*). The dark, small crescentic sclerite (fig. 4, *d.c.s.*) lying vertically on one side near the right phallomere, comes to take a medial position on the ovipositor, and so a firm grip is secured. The male then starts to build up a spermatophore in the pouch of the ejaculatory duct, and when it is fully developed the large endophallus is evaginated and directed towards the spermathecal groove, presumably with the help of the medial virga. In the majority of cases examined the spermatophore was deposited on the left sclerites. This might be accomplished with the aid of the right phallomere.

The Process of Spermatophore Formation.

From the foregoing description it is clear that the three different secretions which build up the various layers of the spermatophore, viz. the transparent, the milky and the translucent layers, can be seen in the three groups of the accessory glands. The first stage in the process is that a certain amount of the milky substance secreted by the long tubules slides into the ejaculatory pouch (fig. 6, *b*). This is slowly surrounded and pressed from both sides by the secretion of the other two sets of tubules. It takes then a medial position and occupies a smaller area of the ejaculatory pouch (fig. 6, *c*). The enlargement of the ejaculatory pouch is directed towards the anterior end.

When the right amounts of secretion have passed, a certain amount of sperm flows from each *vesicula seminalis* into the milky middle layer. Each

sperm mass forms a separate sac. When this last stage has been achieved the spermatophore descends down the ejaculatory duct, its tip that bears the two openings of the sperm sacs is inserted into the spermathecal groove and the spermatophore is laid on the above-mentioned sclerites. A considerable portion of the remaining part of the milky secretion still found in the long tubules is then poured out on the spermatophore and the adjacent sclerites. The couple then separate and take no further notice of each other.

In order to verify Gupta's statement about the mode of spermatophore production, 10 male last-stage nymphs were isolated, each in a one pound jar. They were provided with an ample supply of food and water and kept in an incubator running at 28° C. The adults that emerged were dissected and the accessory glands as well as the ejaculatory pouches were carefully examined at different intervals, ranging from 1-10 days. None of the glands examined

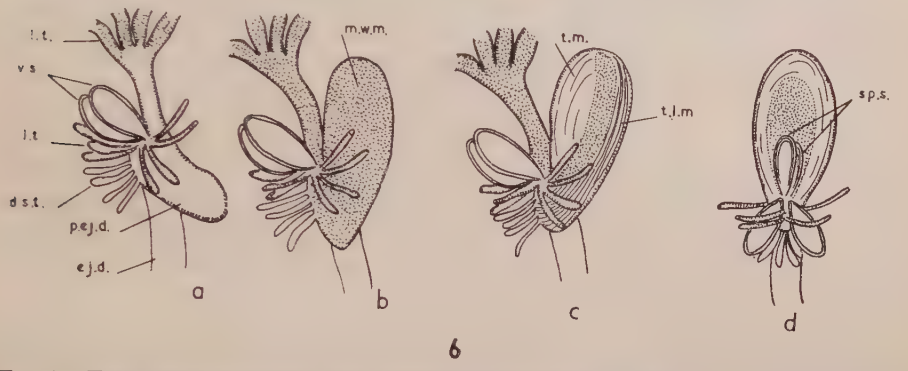


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FIG. 6.—Four diagrams showing the process of spermatophore formation. (*a*) A side view of the male organs before the commencement of the process. For explanation of lettering see fig. 3. (*b*) Filling the pouch of the ejaculatory duct with the milky white secretion derived from the long tubules. (*c*) The deposition of the other two kinds of secretion which surround the milky white mass from both sides, forcing it to take a median position. (*d*) Every vesicula seminalis releases a certain amount of sperm and so two sperm sacs are formed in the milky white mass. For explanation of lettering see fig. 2.

was producing a spermatophore. The ejaculatory ducts as well as the ejaculatory pouches were totally empty, while the tubules of the accessory glands were full of their corresponding secretions. The same procedure was carried out with *P. americana*. Twelve recently emerged males were isolated, each in a similar container. Two had their accessory glands and ejaculatory ducts examined after 5 days from emergence, two were examined after 6 days, two after 7 days, two after 8 days, two after 9 days and the last two after 10 days from emergence. They all had empty ejaculatory ducts. On one occasion a very small amount of secretion slipped into the ejaculatory duct during dissection, and the growth of this mass of secretion could be watched for some time. The same occurred also with *B. germanica*. This certainly happened as a result of water being diffused into the glands, forcing some of their secretion to slip into the ejaculatory duct. Fully developed spermatophores, however, could not be found. There is no doubt, therefore, that in *P. americana*, as in *B. germanica*, a spermatophore develops only during the process of copula-

tion. As *P. americana* has no ejaculatory pouch, nor a spermatophore mould, it is difficult to imagine where the male can keep his spermatophore pending a chance to copulate, and if he does keep it, how such a phenomenon could have escaped the eyes of the great number of authors who have dealt with the anatomy of cockroaches.

It has been claimed by the same author that the conglobate gland plays a part in building up the spermatophore—secreting the outer layer as it is laid onto the female's sclerites. This has never been observed in the *Blattella* spermatophore. The spermatophore is fully developed before it is pushed to the outside. Sections through the conglobate gland before and after copulation show that the lumen of the ducts always contains a very small amount of secretion and it would be very difficult to determine whether this is used during copulation or not.

Finally, it seems that a female receives more than one spermatophore during the span of her adulthood. On several occasions females that had previously copulated were caught in the act of receiving spermatophores.

Summary.

1. Spermatophores have been described by different authors in two species of Blattidae : *Blatta orientalis* L. and *Periplaneta americana* L. That of *Blattella germanica* L. has been described in the present paper from a structural and a developmental point of view. It may well be presumed that spermatophores are of general occurrence in Blattidae.

2. Spermatophores are largely protein ; they are made of the secretion of the highly developed male accessory glands during the time of copulation which extends over a long period.

3. In *B. germanica* three immiscible secretions are poured into the ejaculatory pouch and the sperm are ejected into the middle layer, forming two separate sperm sacs.

4. The spermatophore is held outside the female genital organs by the asymmetrical sclerites lying on either side of the spermathecal groove. After the migration of the sperm to the spermathecae, a process chemically carried out, the spermatophore hardens and is dropped.

5. The part played by the male genital appendages in holding those of the female during copulation is described.

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Book Notice.

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Beside each family in the key is a small sketch of a typical member, and larger figures of whole insects are given in the text. There are hardly any figures of detail. The four coloured plates are exclusively of Lepidoptera.

A TRICHOPTEROUS LARVA WITH A CHELATE FRONT LEG.

By H. E. Hinton, Ph.D.

(*Department of Zoology, University of Bristol.*)

In fast flowing streams at Chaco, Puente de la Via, and Chulumani in the Yungas Valley, Bolivia, I found in June, 1937, several specimens of a Rhyacophilid larva remarkable in having a chelate front leg.[1] Chelate legs have not previously been described in the Trichoptera, nor, so far as I know, in any other endopterygote larvae except in a Dytiscid, *Matus bicarinatus* Say, by Balfour-Browne (1947). In *Matus* both the front and middle legs are chelate. The ventral apex of the tibia is greatly produced and extends nearly as far or slightly further than the apex of the tarsus. The ventral margin of the tarsus and the dorsal margin of the tibia are serrate. The opposed serrate edges do not meet edge to edge in adduction, but to some extent overlap like the blades of a scissors.

In the Rhyacophilid only the first pair of legs is chelate. The ventral apex of the femur is produced, and the part of its dorsal margin opposed to the claw and tarsus is finely serrate (fig. 3). The tibia and tarsus are much shortened as compared with those of the middle and hind legs, and the ventral surface of both segments with the ventral surface of the claw constitute an edge opposed to the edge of the produced part of the femur and overlapping the latter in adduction. The upper edge of the chela thus formed is rounded and not sharp like the lower or femoral edge. The amount of overlap of the two edges is limited by the very stout apical spine on the femur, so that the edge of the claw is contained between this spine and the outer or posterior face of the femur distad from the spine. On the anterior ventral face of the tarsus is a row of four broad tubercles that probably also function to limit the amount of overlap in adduction.

As may be seen from the figures, the femur and trochanter are unusually large, and the trochanter is divided as in nearly all trichopterous larvae. The musculature (fig. 2) is surprisingly little modified as compared with that of a non-chelate leg. The muscles of the telopodite are as follows :

Flexor (*depressor*) *of pretarsus.*—The pretarsal flexor has only two fine strands of muscle arising in the tibia and no fibres arising in the tarsus, whereas in the middle and hind legs of this and all legs of other species one or two strands arise in the femur, and numerous thick bundles of fibres in the tibia. Most of the fibres of the flexor arise in the femur instead of in the tibia, as in non-chelate legs.

Flexor (*depressor*) *of tarsus.*—This muscle is reduced to a single extremely fine strand (fig. 2) that is much more slender than its homologue in the non-chelate legs of the Trichoptera.

Flexor (*depressor*) *of tibia.*—As in non-chelate legs of most larvae, this is the largest of the leg muscles. It has numerous bundles of fibres arising in

[1] Dr. H. S. Ross of Illinois, to whom I sent some larvae, tells me that they belong to the genus *Atopsyche* Banks.

the basal part of the femur and a large bundle in the second trochanter. One of the most constant features of the musculature of the legs of both larval and adult insects is that one of the tibial flexors arises in the trochanter. This

Figs. 1–2.—(1) Anterior or inner view of right front leg of a Bolivian Rhyacophilid. (2) Musculature of same.

muscle has been overlooked by Snodgrass (1935). It has been found in all insects examined that have a well-developed trochanter, i.e. Thysanura (*Pterobius maritimus* Leach), various Orthoptera, Hemiptera, Odonata, Ephemeroptera, Megaloptera, Neuroptera, Coleoptera, and the Panorpoid orders. It is sometimes present when the trochanter is very reduced, as in

larval Lepidoptera. In larval DYTISCIDAE it is usually represented by an extremely fine strand, somewhat difficult to find notwithstanding the fact that the trochanter is large and usually 2-segmented. In *Locusta migratoria* L. and other ACRIDIDAE it is large and distinct in the front and middle legs, but it is apparently absent in the hind legs in which the trochanter is much reduced.

The flexor of the Rhyacophilid arises from a broad and long apodeme which is branched apically, one branch for each of the chief groups of fibres. A small sub-basal area of the apodeme is heavily sclerotized, and this sclerite rubs over a sclerotized invaginated part of the femur, as shown in figs. 2 and 3.

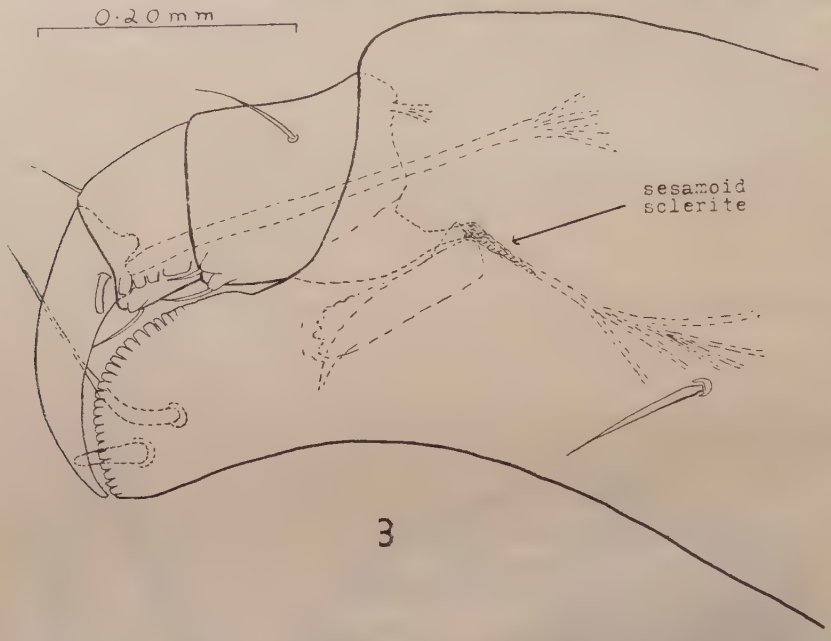

FIG. 3.—Anterior or inner view of distal part of right front leg of a Bolivian Rhyacophilid.

The internal ridge of the femur must affect the direction of pull of the muscle when the latter is contracted. The sub-basal sclerite is an articulating sclerite that, from a functional point of view, is similar to a sesamoid bone in the ligament of a vertebrate. It may be called a *sesamoid sclerite*. Sub-basal or sesamoid sclerites are frequently present in the nearly colourless apodemes of the leg and other muscles of many insects, but in most forms that have been seen they do not rub over internal ridges, as in the species illustrated, but may be simply specially strengthened parts of the apodeme.

Extensor (levator) of tibia.—This consists of a single large bundle arising at about the middle of the femur. In the non-chelate legs of the Trichoptera it consists of several small bundles of fibres that are often relatively shorter. The extensor is always a very much smaller muscle than the flexor.

Reductors of femur.—There are three reductor muscles arising in the trochanter and inserted dorsally near the base of the femur. One of these arises in the first trochanter, and this is also so of the middle and hind legs. The

proximal, and only the proximal, reductor arises in the first trochanter in all trichopterous larvae examined even when the first trochanter is relatively short, as in some species of *Rhyacophila*. The number of reductor muscles is very variable, e.g. *Hydropsyche* sp. has three, *Philopotamus montanus* Donovan and *Polycentropus* sp. four, *Limnophilus lunatus* Curtis five, and *Limnophilus* sp. six. I have examined only the mature larva of these species.

Flexor of trochanter.—In trichopterous larvae this muscle consists typically of three large bundles of fibres, each of which is further divided proximally. The insertions of the three chief groups of fibres are contiguous in most species, but in the Rhyacophilid illustrated and in *Philopotamus montanus* Donovan one of the insertions is slightly separated from the two others.

Extensor of trochanter.—All the fibres of this muscle arise in the basal region of the coxa except for one group that extends into the body and arises near the median line of the sternum. In some other species of Trichoptera this bundle of fibres splits into several minor bundles.

The Rhyacophilid larvae with chelate front legs vary from 5 to 16 mm. in length, and the front legs of the smallest larva are the same as those of the largest. The gut contents show that it is a predaceous species, as are nearly all Rhyacophilidae. I have not seen the larva feeding, but it seems certain that the chelae are used in securing the prey. Balfour-Browne bred *Matus* in an aquarium and never saw them use their chelae in this way. He suggests that the chelae are digging organs, and he has seen them digging into the silt at the bottom of the aquarium. Legs modified for digging are well known in many groups of insects, and all conform to a few basic patterns, and in no instance resemble the chelate legs of *Matus*. The ventral edge of the tibia of *Matus* is serrate, and it is these serrations that may represent modifications for digging. It may be that in its natural habitat *Matus* feeds on some insect larva or oligochaete buried in the mud, but in catching insects free in the water uses only its mandibles like most other Dytiscid larvae. Balfour-Browne has already drawn attention to the swimming hair on the chelate legs. It therefore appears that the legs are not only modified for swimming and grabbing, but possibly also for digging.

My best thanks are due to Mr. J. Balfour-Browne for a larva of *Matus*.

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Snodgrass, R. E., 1935, *Principles of Insect Morphology*. New York.

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